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## THE PROPER DESIGNATION OF THE VASCULAR PLANTS

THEODOR JUST

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The status and growth of taxonomic, morphological and paleontological knowledge of the plant kingdom are to a large extent reflected in the various classifications adopted from time to time. Consequently new advances and viewpoints are likely to result in proposals for certain rearrangements or new alliances which are often accompanied by new designations. Thus it is not at all surprising that in recent years several new names have been proposed for the higher taxonomic unit comprising all vascular plants. These proposals were made despite the fact that in the past the vascular plants had repeatedly been treated as a group. On the other hand, these new names indicate clearly the present revived and increased interest, whether morphological, genetical or otherwise, on the part of botanists in the sporophyte of vascular plants. As a result, a great deal of morphological and anatomical knowledge is now being reexamined and evaluated from many new points of view. This renewed interest is, then, the direct outgrowth of the many remarkable advances made in morphology, paleobotany, genetics and other fields.

It seems desirable, therefore, to consider at this juncture the more important designations proposed for the vascular plants together with the criteria and evidence claimed in their support. Curiously enough, several of these designations were not published in conformity with the International Rules of Botanical Nomenclature and thus must be regarded as *nomina nuda* (see especially Recommendation viii and Article 37). Without attempting an exhaustive treatment of all designations published since the beginning of modern botany (Winckler, 1854, du Mortier, 1864, Gmelin, 1867), the following discussion should illustrate the difficulties attending the selection of a suitable name in this as well as similar cases and



the desirability of having the entire problem of the names of higher categories presented at the next International Botanical Congress. Strict application of the Rules to many widely used names of higher categories, old or new, will inevitably result in a long list of *nomina conservanda*.

Apparently A. P. De Candolle was the first botanist who grouped all vascular plants together as "végétaux vasculaires" (1805)<sup>1</sup> and referred the others to "végétaux cellulaires". The name "Plantae Vasculares", proposed by him for this group in 1818, has as such, or abbreviated to "Vasculares", been widely adopted in floras, manuals and other systematic treatises. However, dissatisfied with his own disposition of the ferns and fern allies, he removed them later (1833) from the Monocotyledoneae among the vascular plants and erected for them the new group "Semi-vasculares", which in turn was relegated to a place among the cryptogams or cellular plants. Noteworthy in this connection is also the opening statement of the Latin diagnosis (De Candolle 1818, p. 121) which reads as follows: "Plantae contextu celluloso vasisque lymphaticis constantes; stomatibus instructae"; *etc.* De Candolle was firmly convinced that this classification (1833) was correct, because the study of vegetative (vascular *vs.* cellular plants) as well as reproductive organs (Cotyledoneae *vs.* Acotyledoneae) had led him to distinguish equivalent groups. Although nomenclaturally speaking, "Plantae Vasculares" is a valid name legitimately published, the somewhat ill-defined or often erroneous anatomical concepts of that time and the ideas of relationship held by its author are, in part at least, responsible for the appearance of many later designations.

In subsequent classifications, especially those following Hofmeister's classical researches, vascular plants appear as a part of a larger entity such as "Cormophyta", "Prothallatae", "Embryophyta", and "Archegoniatae." There can be no doubt that, morphologically speaking, the gap between the thallophytes and all other groups—here conveniently though inappropriately included in Schaffner's "Metathallophyta"—is probably the largest known of any major plant groups. For this reason the similarities of all higher plants appear much greater if viewed on the basis of their

<sup>1</sup> Alph. De Candolle corrected the dates of publication of "Flore Française"; only the last volume was issued in 1815, whereas the others were published in 1805. See *Ber. Deut. Bot. Ges.* 7: 394, footnote 2, 1889.

homologies than if studied from some particular viewpoint and certainly if compared with the numerous unrelated groups customarily referred to the thallophytes. It should be remembered, however, that the term "Thallophyta", despite its wide use in textbooks, is today outmoded, irrespective of the fact that it continues to be a convenient term needed to indicate concisely a certain morphological level. If this is recognized, "Thallophyta" can never be considered cognate with natural groups which include only related forms. Consequently, several authors have dropped "Thallophyta" as a major group and substituted for it a number of independent phyla (Bessey, Engler, Fritsch, Pascher, Schaffner, Smith, Wettstein, *et al.*).

The metathallophytes, on the other hand, have been treated as a larger unit or divided into separate phyla (Berry, Bessey, Eichler, Engler, Haeckel, Schaffner, *et al.*). Disregarding here the now inadequate Linnaean distinction of "Cryptogamae" and "Phanerogamae", the problem involves mainly the nature of the evidence supporting either the maintenance of two or more divisions or phyla, or their inclusion in a major category. Thus phylogenetic or other considerations have at different times led to the proposal of very large divisions made up of thallophyte and metathallophyte members or groups. The following examples may illustrate this point.

Using the presence or absence of sexuality and of spore-producing structures as the principal criteria, MacMillan (1892) proposed the term "Sporophyta" for all groups with sexual reproduction and sporophytes (higher algae, fungi to Angiospermae). This usage of "Sporophyta" obviously differs from the very opposite application of it to all spore plants, formerly known as "Cryptogamia" (Willkomm, 1854). Hallier (1905) used "Sporophyta" in still another sense by restricting it to the pteridophytes. Needless to say, little can be gained by such confusion.

Thallophytes and bryophytes also have been combined at different times and for various reasons. For instance, Bugnon (1922) called them "Cytophytes", or, like some older botanists, "Cellulaires". In the same year Gravis recommended replacement of the terms "gametophyte" and "sporophyte" with "gametophore" and "sporophore" and recognized two major groups, namely, "Gametodynames" with dominant gametophytes (phycophytes and bryo-

phytes) and "Sporodynes" (pteridophytes and spermatophytes) with dominant sporophytes. Our present knowledge of the life histories of many lower plants certainly disposes readily of such an attempt to utilize the relative development of gametophytes and sporophytes as the sole criterion of classification of major groups.

Other attempts of combining thallophytes and bryophytes were based largely on organographic evidence. Thus van Tieghem (1906) called all plants without roots or vascular elements "Arhizophytes" or "Invasculaires", whereas those plants which bear roots and contain vascular tissue were designated "Rhizophytes"<sup>2</sup> or "Vasculaires". Later Troll (1937) accepted the distinction of rhizophytes and arhizophytes and pointed out that the morphology of the root provided the only criterion for the typological characterization of the pteridophytes and spermatophytes. On this basis he designated the former as "Homorhizophyta", whose roots arise as lateral organs from the shoot, and the latter as "Allorhizophyta", whose embryo has two growing points, one of which gives rise to the primary root.

The worst professedly phylogenetic system proposed in recent years is based solely on the presence or absence, the character and number of flagella found on reproductive organs throughout the plant kingdom. According to its authors, Sakisaka and Sinoto (1930), phylum 4 or "Polycontophyta" apparently includes all metathallophytes in strange new alliances. The last subphylum of this phylum, the "Stephanokontae", made up of the Oedogoniales and Derbesiales, apparently represents the climax of the plant kingdom.

Many botanists are now agreed on dismembering the old subkingdom Thallophyta, but are still in disagreement on treating the metathallophytes as a natural entity or as two or more distinct phyla. Unger (1838) was the first to contrast "Thallophyta" (plants without axes) with "Cormophyta" (plants with axes). This distinction was immediately adopted by Endlicher (1840), although the term "Cormophyta" has since been applied in various ways. For instance, Alexander Braun (1864) as well as Arber (1921) used it for the pteridophytes, and Haeckel (1894) for the vascular plants, whereas Lotsy and Wettstein applied it to the entire meta-

<sup>2</sup> Rudolphi proposed the term "Rhizophyta" in 1830 and applied it to fungi and lichens (fide Zunck, 1840). Van Tieghem's term is therefore a later homonym.



thallophyte complex, as originally defined. As pointed out above, since more evidence can be presented in favor of the unity of the metathallophytes than that of the thallophytes, the term could well be applied to this subkingdom in Endlicher's sense and as redefined by Lotsy and Wettstein, if the other subkingdom is to be called "Thallophyta". Given this interpretation these terms would at least be cognate, because they would be based on the same criterion, *i.e.*, the structure of the plant body as a whole. Even without retaining "Thallophyta", "Cormophyta" should be used as the oldest available name for the metathallophyte complex (Wettstein, 1935) rather than in Haeckel's restricted sense for the vascular plants.

Engler's widely accepted term "Embryophyta" (1886) is, by comparison, based on the fact that in all metathallophytes zygotes invariably develop into multicellular embryos while confined in female sex organs and that the plants are capable of continued growth or continued embryology. However significant these characters may be, they pertain first of all to a stage in the life history of these plants and not to the plant as a whole; also their "continued" embryology (continuous presence of formative tissue) is more effective in the spermatophytes than in the pteridophytes (except the Psilophytales) and is absent from the bryophytes (Bower, 1930).

Similar arguments might be advanced with reference to the use of the term "Archegoniatae" s.l., applied as a synonym of "Embryophyta" by Conard (1919) and Torrey (1932). Another point would be that "Archegoniatae" s.s. has long been used for the combination Bryophyta and Pteridophyta (Engler, Bower, Wettstein, *et al.*) or for these two groups and the Gymnospermae (Kousnetzow, 1922), irrespective of Nilsson's (1941) efforts to reaffirm the archegoniate nature of angiosperms. Even those who place the bryophytes side by side with pteridophytes and spermatophytes admit the numerous similarities existing between bryophytes and pteridophytes. Surely "Archegoniatae" s.s., also called "Prothallophyta" (1866) and later "Diaphyta" (1894) by Haeckel, should be dropped only if the vascular plants deserve to be grouped together in preference to the classifications based mainly on gametophyte characters. Harder (1939) expresses this opinion clearly and states that, although no direct connections between bryophytes and pteridophytes are known and the latter are related to the sper-

matophytes (both have tracheids, etc.), a distinction into cellular *vs.* vascular plants in the De Candollean manner would obscure the relationships existing between bryophytes and pteridophytes.

After this account of the most commonly used designations of the entire metathallophyte complex, a discussion of the terms proposed for the vascular plants as a unit of varying extent is now in order. In addition to the terms and classifications discussed above, the following proposals are of interest here. Stolley (1925) removed the Psilophytales from the Pteridophyta and placed them below the Bryophyta with a rank equal to these two groups, the Pteridospermae, Gymnospermae and Angiospermae. The viewpoint expressed in this arrangement approaches that of Church (*vide* Brown, 1935) who regards the Rhyniaceae as primitive Bryophyta, whereas Arber (1921) is of the opinion that "Procormophyta" are "half-way between the Thallophyta and Pteridophyta". These dispositions of the Psilophytales failed to gain recognition and acceptance, however.

Pascher's (1931) term "Pterido-Anthophyta" is in reality no more than a compromise. Similarly, Haeckel's (1894) distinction of "Cellophyta" (= Bryophyta) and "Vasophyta" (= Pteridophyta and Spermatophyta) as well as Bugnon's (1922) distinction of "Gametophyteae" (Gamètophytées = Bryophyta) and "Sporophyteae" (Sporophytées = vascular plants) do full justice neither to the problem at hand nor to the newer knowledge of the lower plants. Such terms are at best misnomers. Conard's (1919) division of the "Embryophyta" into "Atracheata" (Bryophyta) and "Tracheata", which reflects Jeffrey's views, marks a great improvement over earlier proposals and was therefore adopted by Torrey (1932). Unfortunately these designations might easily be confused with names long in use in zoological classifications, irrespective of other considerations discussed below.

Van Tieghem's term (1906) for all vascular plants, "Rhizophyta", was restricted by Bugnon (1922) who removed the rootless members found among the earliest Psilophytales and placed them in the "Thalloxylophytes". Although certain living pteridophytes are also rootless, Troll (1937) claims that their embryo structure is such that, if roots were present, they would develop like those known in other pteridophyte forms. The reader is referred to Bower (1935) and Schopf (1943) for more detailed discussions of the "primitive spindle" and its significance in this connection.



Another designation, first published by Sinnott (1935) and later used by Eames (1936), Foster (1941), Tippo (1941), Darrah (1939, 1942), and MacDougall and Hegner (1943), is "Tracheophyta",<sup>3</sup> which is regarded as "cognate with ThallopHYta and Brypophyta" and includes "the vascular plants as a whole." It is based on the appearance in vascular plants of "tracheary elements" and not primarily on the fact that the elaboration of the sporophyte was made possible by the development of the conducting system. Since tracheary elements are basic constituents of the xylem of all vascular plants, the more inclusive term "Xylophyta", though originally proposed by Clements (1902) for ecological usage of limited applicability, was actually applied to all vascular plants by Bugnon (1922) and Stefanoff (1937). These designations, viz., "Tracheata", "Xylophyta" and "Tracheophyta", indicate the great importance now attributed to the tracheary elements in the evolution of the sporophyte of vascular plants, which is also well substantiated by the paleontological record (Hofmann, 1934).

One more term remains for consideration in this connection. Like others it too was proposed by its author in a rather casual manner. In his review of Zimmermann's well known book on the phylogeny of the plant kingdom (1930), Pia (1931) recommended a different treatment of the "Cormophyta" from that adopted by Zimmermann and suggested the term "Stelophyta" for the vascular plants.

Undoubtedly this term would be acceptable only as long as the stelar theory is held in high regard by botanists.<sup>4</sup> In Wardlaw's opinion (1944), the older botanists dealt with the "*individual strand* as the unit of vascular construction", whereas "van Tieghem (1886) recognized the *vascular system*, whether compact and simple or disintegrated and complex, as the unit. This he called the stele. It was a conception which, like one that had already been formulated by Sachs, tended towards a recognition of the essential unity of the shoot". Eames and MacDaniels (1925) assessed the influence of the stelar theory on botanical knowledge in the following way: "the establishment of the stelar theory has supplied a basis for an

<sup>3</sup> Although this term seems to have been used long before it was published, it is apparently impossible at this time to determine the author of it (A. J. Eames in litt.).

<sup>4</sup> Moll (1934, footnote on p. 313) points out the different meanings which have been attributed to the word "theory" as used in the combination "stelar theory".

understanding of the structure of the plant body such as was not possible before. This alone has brought the vascular skeleton to the front as of much importance in the study of phylogeny". Granted that many objections to details of the stelar theory have been raised (Campbell, 1940; Watson, 1943; *et al.*) and disproved (Rudolph, 1921; Schoute, 1926, 1938; Smith, 1938), and the discussion of the nature and origin of stem, leaf and root has not yet completely subsided (Eames, 1935; Cappelletti, 1936; Bower, 1930, 1935; Zimmermann, 1930, 1938; Arber, 1941; Wetmore, 1943; Wardlaw, 1944), these conditions need not affect the possible acceptance of the term "Stelophyta" any more than similar situations have affected the use of other terms such as "Anthophyta", "Spermatophyta", "Spermaphyta", "Angiospermae", *etc.* In addition, Smith (1938) shows that the discovery of the most primitive land plants confirmed the essential postulates of the stelar theory long after its original pronouncement and subsequent elaboration, and Bower (1935) concludes that "the vascular tissues provide the most constant characters of the plant body".

It may not be entirely out of place to mention here that the phenomena of alternation of generations, sex determination and heterospory are currently being subjected to experimental studies and that new interpretations are gaining ground (Schiffner, 1925; André, 1938; Pincher, 1935, 1937; Thomson, 1934; *et al.*). Many supposedly well established concepts are bound to be replaced in this process. Some day perhaps even the architecture of the plant body and the morphogenetic processes bringing it into being will become clear in all their ramified complexity, since many primitive land plants are already fairly well understood (Zimmermann, 1938). At that time a new designation based on external morphological characters may again become desirable, but it should be better than Cohn's "Pteridophyta" (1872) which was never the best designation for the habit of the fern allies.

In conclusion it may be pointed out that, unless convincing proof of the valid status of one of the older designations can be furnished, botanists are apt to look for a new term. Unfortunately, according to the International Rules of Botanical Nomenclature, the more recently proposed designations, *viz.*, "Xylophyta", "Stelophyta" and "Tracheophyta", are *nomina nuda* which can not be used as such. Nevertheless, the last of these *i.e.*, "Tracheophyta", has gained

limited acceptance, predominantly in morphological literature. With few exceptions most designations of the higher category including all vascular plants are based on anatomical characters of varying significance, the most general term being "Stelophyta", whereas "Tracheophyta" is the most specialized of the group. The case of the proper designation of the vascular plants illustrates the great need for consistent application of the International Rules of Botanical Nomenclature to the names of higher categories and for a critical review of the most widely accepted terms by the Subsection of Nomenclature of future International Botanical Congresses.

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# ABSORPTION OF WATER BY PLANTS

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## INTRODUCTION

This review is concerned primarily with the nature and origin of the forces bringing about movement of water from soil or other media surrounding roots into the conducting elements of the xylem, and with those internal and external factors which affect the rate of such movement.

Absorption of water is not an independent process, but is closely related to other processes included in the domain of plant water relations. The rate of water intake is markedly affected by the rate of transpiration and by the extent and condition of the root systems. It is also affected by such environmental factors as the available moisture content of the soil, soil temperature, soil aeration, and to a lesser extent by the kind and concentration of ions in the soil.

Some phases of the work discussed in this review naturally are incomplete and do not permit formulation of definite conclusions concerning certain aspects of the absorption problem. Where the writer has drawn conclusions or made generalizations they seem to be those most justifiable on the basis of the available evidence. It is realized, however, that as knowledge of these processes increases it may be necessary to modify some of the present conclusions. It is impossible to cite all the literature, but most of the papers cited have bibliographies in which the reader can locate other papers dealing with any particular phase of the field.

## ABSORPTION MECHANISMS

### *The Existence of Two Absorption Mechanisms*

Intake of water by roots apparently is brought about by two quite different and independent mechanisms which probably do not even operate simultaneously. When soil moisture is abundant and transpiration is slow, absorption frequently exceeds water loss, resulting in the development of hydrostatic pressure or "root pressure" in the xylem. Since this type of absorption occurs only in plants with healthy roots, and according to some



theories is dependent on the expenditure of energy by cells of the roots, it has been termed "active absorption" (212). The mechanism responsible for active absorption and the resulting guttation and exudation from cut stems will be discussed later.

The situation existing in the water-conducting system of rapidly transpiring plants appears to be quite different from that existing in well watered, slowly transpiring plants. During periods of deficient soil moisture or when the rate of transpiration is moderate to rapid no root pressure or exudation can be demonstrated. Instead, the pressure on the water in the xylem vessels is nearly always lower than atmospheric pressure, as evidenced by instantaneous penetration of liquids into incisions made in the xylem of such plants. Under such conditions the roots appear to act simply as passive absorbing surfaces for water, as evidenced by the fact that transpiring plants can absorb considerable water through dead roots (137). This type of water intake has therefore been termed "passive absorption" (212) to distinguish it from absorption which is dependent in some manner on the activity of living root cells.

The relative importance of active and of passive absorption has been warmly debated. After describing the two mechanisms evidence concerning their relative importance in growing plants will be presented.

#### *Active Absorption and Root Pressure Phenomena*

*Species from which exudation occurs.* Sap for beverages has been obtained for centuries from palms and agave, and the first settlers of New England found the Indians tapping sugar maples and boiling down the sap. Exudation from grapevines has also been known for many centuries, but according to Sachs (228), Hofmeister (112) was the first to demonstrate that exudation commonly occurs from the stumps of many cultivated herbaceous species. No recent attempts have been made to list the species exhibiting root pressure, but it certainly occurs in scores and probably in hundreds of species (54). Wieler (268) collected from the literature references to "bleeding" or "weeping" in 126 species belonging to 93 genera and 47 families, distributed among the ferns, gymnosperms and angiosperms, and added from his own observations 62 additional species. Many species are included

by Wieler which probably do not really exhibit root pressure, as he apparently included exudation from glandular hairs, woody tissue, and even from root systems previously soaked in salt solution. Several conifers were listed, for example, but none of them is known normally to exhibit true root pressure. It has been produced artificially in certain coniferous species by first soaking the root systems in salt solutions, then transferring them to pure water (77, 268). It has not been determined whether the absence of root pressure in various species is the result of anatomical or of physiological conditions.

*Types of exudation.* Considerable confusion has resulted from failure to distinguish between exudation caused by root pressure, exudation caused by local stem pressure, and that caused by the activities of special cells such as those of glandular hairs. Wieler (268) seems to have treated all types of exudation of liquid as examples of "bleeding", but Clark (42) and Sachs (228) had already distinguished between exudation caused by root pressure and exudation caused by pressure developed in the stems of woody plants. It is probable, for example, that the exudation of sap from a wounded grape or birch stem is caused by root pressure because it occurs only after the soil has warmed up in the spring and after the temperature remains continuously above freezing. Furthermore, it continues rather steadily, day and night instead of fluctuating with temperature as does maple sap flow (126). Exudation of sap from the sugar maple, on the other hand, is probably largely or entirely caused by local stem pressure resulting from increasing temperature (42), though some investigators believe that the activity of living cells must be involved (126). Maple sap flow usually will occur any time in the winter that a cold night is followed by a warmer day with temperatures above freezing, and it ceases abruptly in the spring when wide variations between day and night temperatures cease, just when sap flow from birch and grape is beginning. By attaching gauges to maple roots it was found that positive root pressures were too infrequent and too slight to account for the flow of sap from tapped trees (41, 42, 126). Molisch (188) regarded the stem pressures and exudation reported in trees by Hartig and Figdor as caused by activity of cells in the immediate vicinity of the wood and not by root pressure. The flow of sap from

palms following removal of the inflorescence was also regarded by him as a local secretion because it is maintained only by repeated wounding, and, furthermore, because root pressure is not generally observed in the lower part of the stem of palms. Exudation from wounds in stems of cacti and Monterey pine are also said to be caused by the activity of living cells in the immediate vicinity of the wounds, and no root pressure was ever observed in pine (169, 170). There has been some debate concerning the occurrence of root pressure in aquatics, but Thut (247) reinvestigated this problem and found that measurable quantities of sap exuded from cut stems of several species of submerged aquatics, largely as the result of root pressure. It is generally agreed that most guttation is caused by root pressure, although drops of water are sometimes secreted from modified epidermal cells and multicellular hairs (91).

This review will be concerned primarily with exudation of liquid caused by pressure originating in the roots. Secretion by glands and exudation caused by local stem pressures will receive only incidental consideration.

*Volume of exudate.* The volume of exudate depends on the size and type of plant, the ratio of absorption to transpiration and on various environmental factors, especially temperature and available soil moisture. Sugar maples may yield five to six liters of sap in a single day and 25 to 75 liters in a season. Ironwood and birch are said to yield larger volumes of sap than sugar maple, a paper birch 37.5 cm. in diameter having produced about 28 liters of sap in one day and 675 liters during the season (42). The agave is also said to yield hundreds of liters of sap over a period of several weeks. Sachs (228) writes of a sunflower plant about three meters in height with a stem diameter of four to five centimeters which exuded 1,061 ml. of sap from the stump in 14 days, or a volume of sap about three times the volume of the entire root system. Sugar cane stools have been observed to exude 100 ml. or more of sap per day for a week or longer after detopping (263), and corn plants in the milk stage have yielded over 500 ml. of sap in three days and over 1,700 ml. in 15 days (164). Four squash plants grown in nutrient solution and transferred to tap water yielded over 550 ml. of sap in 24 hours, though the total fresh weight of their root systems was only 450 grams. The



volume of sap exuding from these root systems in 24 hours was thus greater than the total volume of the root system and amounted to more than five times the estimated volume of the lumina of the xylem vessels (54).

*Composition and osmotic pressure of exudate.* The liquid exuding from cut stems and hydathodes is not pure water, but contains varying proportions of carbohydrates, nitrogenous materials, organic acids and mineral salts. The sap of the sugar maple contains an average of over 3% sucrose and small quantities of proteins, minerals, especially calcium and potassium salts, and organic acids, especially malic acid (128). The principal carbohydrate in birch is said to be glucose (41), and an analysis of grape sap gave a total of 1.56% solids, 0.56% being ash, 0.56% organic acids, 0.33% reducing sugar, and small quantities of organic and inorganic nitrogen (204). Weller (263) has published analyses of sap from Hawaiian sugar cane, Pierre and Pohlman (200) summarized the analyses of several investigators and Anderssen (3) cites a number of investigations of woody species. Practically all these data were based on sap exuding from cut stems.

Since woody species usually exude sap only for a limited period in the spring, attempts have been made to obtain samples of xylem sap at other seasons by centrifuging (7) and by the use of liquid or gas pressure (3, 12). Sap centrifuged from the xylem of several woody species in Ireland had osmotic pressures of about 0.5 to 1.5 atmospheres (67, 68). In general, the concentration of solutes was highest in early spring, was very low during summer and early autumn, increased slowly during the winter and suddenly reached its peak again in the spring. Similar changes in concentration were observed in sap extracted by air pressure from apricot and pea stems in California, though the concentration level was lower (3).

The possibility of analyzing the sap exuding from the stumps of detopped herbaceous plants and using the results as a guide in determining the adequacy of the supply of minerals has been discussed by several investigators. Xylem sap obtained from corn has a composition much nearer the composition of the soil solution than does sap expressed from the tissues (164). It has been found to give a good measure of phosphate supply and

probably is a good indicator of the available supply of nitrogen and potassium (200). Considerable discrepancies existed between the composition of the exudate from sugar cane and the composition of the soil extract (263). One investigator (153) suggested that the best method of obtaining samples of soil solution is to displace it through plant root systems by air pressure. It has been suggested that the concentration of certain elements, especially nitrate nitrogen, in the conducting system may affect the growth of microorganisms and the severity of certain diseases of the vascular system (232).

*Magnitude of root pressure.* The first measurements of root pressure known to the writer are those of Hales (92) who observed pressures of more than one atmosphere in grape. Pressures of 2.6 atmospheres have been reported for birch in New England (41, 181), and according to Huber (117) a Japanese found *Cornus controversa* to develop a maximum pressure of over 1.9 atmospheres. The maximum pressure developed by sugar cane was 1.9 atmospheres, and the most drought-resistant varieties maintained the highest pressures during periods of decreasing soil moisture (263). It was reported that excised tomato roots growing in culture solutions exude sap with a pressure in excess of six atmospheres and probably equal to at least ten atmospheres (265). This probably is the highest true root pressure ever recorded and is the more remarkable because it was produced by isolated roots only a few centimeters in length. Boehm (18) and Figdor (78) observed pressures of over eight atmospheres in stems of woody species, but Molisch (188) claims these pressures were of local origin, and MacDougal (170) says the four-atmosphere pressure observed by him in Monterey pine was also of local origin and not caused by root pressure.

Sap exuding from wheat seedlings is reported to have an osmotic pressure of about 1.3 atmospheres (166), and a Russian (227) by indirect means calculated the exudation pressures of various herbaceous species to range from 0.5 to 1.5 atmospheres. Magnitude of root pressure is affected by the environment of the roots, none being observed in cold or dry soil, or in a poorly aerated medium. The root pressure of tomato plants grown in full strength Hoagland solution was higher than that of plants grown in half strength solution, the maximum root pressure observed being about two atmospheres (250).

*Periodicity of exudation.* Ever since the early studies of Hofmeister (112) investigators have observed fluctuations in magnitude of root pressure and volume of exudate which seemed to occur independently of variations in the environment (87, 108, 218, 239, 265, 268). Grossenbacher (88) showed that in sunflower there is a well defined periodicity with a maximum and a minimum each 24 hours, the maximum value coming during the day, the minimum at night. If plants are grown in darkness with artificial light supplied only at night the cycle is shifted so that the maximum occurs during the artificial day. The 24-hour cycle also exists in plants when grown with continuous artificial light, but the time of occurrence is determined by the time at which the plants are detopped. No satisfactory explanation of the causes for this definite periodicity can be offered (238). Considerable variations in the volumes of water absorbed and exuded by excised onion roots and root segments have also been observed by Rosene (222) who also found the ratio of absorption and exudation was quite variable at first, but usually reached unity in 24 hours.

*Tissues involved.* It is ordinarily assumed that root pressure is developed in the water-conducting elements of the xylem and that the exuding liquid comes from the open ends of these elements. This view was challenged by two English investigators (123) who claimed that exudation occurs from the phloem of *Acer pseudoplatanus* L. Exudation from the phloem has been observed in some species (54, 61, 65, 118, 193), but it is usually most abundant in woody species in late summer (191), and the quantity of sap obtained is very small compared to that obtained from the xylem in the spring. Other European workers who reinvestigated this problem reported sap to exude only from the xylem of birch and *Sanchezia nobilis* Hook (116, 121). The writer found clear evidence that in the spring exudation occurs only from the xylem of wounded *Acer rubrum* L., *Betula nigra* L. and *Carpinus caroliniana* Walt., and exudation from the xylem has been observed in numerous herbaceous species which have been carefully observed (54, 143). It appears that the English investigators misinterpreted their results because they failed to take into account the marked diurnal variations in sap flow caused by the alternation of positive and negative pressures in the water-conducting system of woody plants.



*Guttation.* By far the most common and conspicuous manifestation of root pressure is the exudation of drops of liquid from the edges and tips of leaves, a process termed "guttation" by Burgerstein (32). Guttation occurs through hydathodes which consist of stomate-like pores in the epidermis below which are large chambers surrounded by masses of thin-walled parenchyma cells. The xylem of a small vein terminates beneath each hydathode, and presumably root pressure forces water out of the xylem, flooding the intercellular spaces and causing an overflow through the pores to the exterior of the leaf. Guttation also occurs through ordinary stomates of some grasses and legumes, and secretion independent of root pressure occurs from various specialized epidermal cells and hairs (91, 156). Haberlandt (91) distinguished between epithem hydathodes from which water is forced by root pressure and active hydathodes from which water is secreted by forces developed in the cells themselves. It seems preferable to term the active hydathodes "glands" and the outflow of liquid "secretion", since the force responsible for it is entirely different from that causing guttation from epithem hydathodes. While most plants exude only a few drops of water during an entire night, species of *Colocasia* have been reported to exude from 10 to 100 ml. in a night. Although *Colocasia antiquorum* is said to exude almost pure water (69), the guttation liquid usually contains low concentrations of sugar and salts (58, 60, 270), and that of certain species contains so much salt that the leaves become incrustated. Instances have been reported of injury to leaves, in the nature of tipburn, by concentration of solutes caused by evaporation of the guttation water and also by solution of spray materials in the water which is sometimes reabsorbed into the leaves (59, 122). It is also claimed that conditions favorable to guttation often result in water-soaking of the leaves, facilitating infection by pathogenic organisms which otherwise would have difficulty in gaining entrance (125).

More recent investigations have substantiated the long-held opinion that guttation is caused chiefly by hydrostatic pressure originating in the roots (190, 271). Montford (190) regarded guttation as a sensitive indicator of the availability of water to plants and used it in his studies of the water relations of bog plants. Gäumann (84) also regarded it as a valuable indicator

of the condition of the roots. Leonard (154) has recently used change in root pressure as a measure of injury to cotton root systems by cultivation.

Guttation is most common in plants growing in moist warm soil with their tops surrounded by humid air. It occurs only when absorption is sufficiently in excess of transpiration to cause development of a positive pressure in the xylem elements. Conditions which hinder water intake, such as cold or dry soil, a high concentration of solutes and the presence of toxic substances, also conditions which favor high transpiration, reduce or prevent guttation. These factors will be discussed in more detail in connection with factors affecting water intake.

An interesting example of exudation of water from uninjured woody stems of red maple, analogous to guttation, has been reported (82). In late February sap was observed exuding through the bark of stump sprouts at a height of six to eight feet. It probably escaped through lenticels. Escape of sap from the leaf scars of deciduous species has been observed during warm humid autumns in Louisiana (208).

*The root pressure mechanism.* No phase of botany has caused more discussion and controversy than the causes of root pressure and the resultant guttation and exudation from woody stems. As Heyl (108) stated in his extensive review, this is partly because of lack of agreement concerning what is to be included under root pressure. Such diverse phenomena as secretion from nectaries and from digestive glands of insectivorous plants, guttation, flow of sap from wounded agave, palm and sugar maple plants and from detopped root systems have all been included by some writers. It is highly doubtful that all these phenomena have the same cause, and it is, therefore, not surprising that different investigators have come to different conclusions. As previously indicated, this discussion is chiefly concerned with pressures which originate in the root system and with the direct results of these pressures on other parts of the plant.

The principal explanations of root pressure which have been offered may be placed in two groups, those which are based on some sort of secretory activity by the root cells and those which assume that the roots behave essentially as osmometers.

*a. Vital or secretion theories of root pressure.* In accord with

the vitalistic philosophy of the times, most early explanations of root pressure assumed some sort of secretory activity of the root cells. One of the earlier definite theories was that of DeCandolle (63) who believed the root tips, which he termed "spongioles," were contractile organs which sucked in water and forced it into the xylem. His theory somewhat resembles that of Bose (20) which received wide publicity a few years ago. Bose claimed that "the absorbing root-cells are continuously stimulated by mechanical friction against the soil, giving rise to peristaltic waves of pulsation along the active propulsive layer of the inner cortex". Hofmeister (112) first reported the occurrence of root pressure in herbaceous plants and first observed periodicity in amount of exudate and pressure. He believed that absorption of water by the parenchyma cells of the roots and the resulting turgor pressure caused a unilateral movement of water through these cells and its expulsion from the inner cells into the intercellular spaces and the xylem vessels. Wieler (268), Pfeffer (199), Lepeschkin (155) and others believed that root pressure occurs because the root cells are more permeable on the inner than on the outer side and therefore absorb water from the exterior and lose it to the xylem on the interior of the root. It was suggested by Ursprung (249) that a difference exists in the suction tension (diffusion pressure deficit of Meyer, 183) on the inner and outer sides of the endodermis which is capable of causing the movement of water across the endodermis into the xylem. Several investigators have suggested the importance of differences in electrical potential between the inside and outside of the root. If the tissues in the stele have a lower potential than the tissue near the epidermis, *i.e.*, are negative to the external tissue, then water might move inward by electroosmosis. Stern (241) caused water to move through segments of willow twigs by artificially producing a difference in potential between the two ends. Differences in electrical charge on the inside and outside of the endodermis have been reported, based on staining techniques (9, 130), and Lund (165) found differences in potential across the cortex of roots which he believed might cause the inward movement of water and root pressure. After extensive review of the literature and experimentation Heyl (108) concluded that root pressure is not a simple osmotic process but is probably an electro-osmotic phe-

nomenon in which a potential difference is maintained by means of energy released by respiration of the root cells. It has also been claimed that there is a good correlation between rate of respiration and rate of water absorption by corn roots (105), but another investigator has failed to observe such a correlation (163).

Renewed interest in the possible role of secretion has been aroused by claims that the cytoplasm sometimes "secretes" water into the vacuoles (13, 167, 178). It also has been reported that the intake of water by detopped root systems and excised roots can be partly inhibited by KCN (225, 250). Exposure of roots to KCN not only inhibits water intake but also decreases oxygen consumption, suggesting that water intake and the resulting root pressure are dependent on energy supplied by respiration in the root cells (225). Since inhibition is only partial, Van Overbeek (250) concluded that root pressure is caused by two forces, a simple osmotic process not affected by cyanide and a secretory process inhibited by it. Rosene (225), however, suggested that failure to completely inhibit the root pressure mechanism may be because KCN does not completely inhibit respiration. More recent work (57) does not support the view that water is secreted into the vacuole, and it is possible that the inhibiting effect of KCN on root pressure is indirect and caused by reduction of solute accumulation in the roots rather than by inhibition of any secretory mechanism.

*b. Osmotic theories of root pressure.* Our present day views on plant water relations are strongly influenced by the work of Dutrochet (73) who developed the theory of osmosis and applied it to numerous plant processes. He was somewhat vague, however, concerning the details of the osmotic explanation of root pressure, and during the latter part of the 19th and early part of the 20th century most botanists preferred some sort of explanation based on secretion into the xylem. This was largely because of inability to understand how water could move from the parenchyma cells surrounding the xylem into the vessels. It was assumed that water moves only along gradients of increasing osmotic pressure, and it was therefore difficult to explain how it could move from the living cells surrounding the xylem elements, which have an osmotic pressure of several atmospheres, into the xylem elements whose contents usually have an osmotic pressure of less than two



atmospheres. The first really workable osmotic theory seems to be that proposed by Atkins (7) who stated "that the influx of water from the ground to the elements of the wood of the roots takes place across the cortical cells of the root. For though they have a much higher osmotic pressure than have the tracheae they function merely as a complex, semipermeable membrane as they are already fully distended". It is now generally agreed that movement of water in plant tissue occurs along gradients of diffusion pressure deficit (hereinafter to be termed D.P.D., following Meyer, 183) which may be largely independent of the relative osmotic pressures of the cells (17, 202, 246). Another problem still existed, however, with respect to the maintenance of a sufficiently high concentration of solutes in the xylem to cause a gradient of diffusion pressure deficit across the cortex from soil to xylem. Atkins (7) suggested that the adjoining parenchyma cells secrete sugar into the xylem vessels, thereby maintaining the necessary concentration of solutes. Priestley (202) believed that these solutes might be supplied from the contents of cells which are differentiating into xylem vessels.

Recently an interdependence between root pressure and ion absorption has been proposed by Crafts and Broyer (55). Since ion absorption and retention are related to rate of metabolism and that in turn to oxygen supply, the tissue in the interior of the root is less able to retain a high concentration of ions than the better aerated tissue at the periphery. A gradient therefore should exist across the root tissues normally accompanied by loss of solutes from the innermost parenchyma cells into the xylem vessels, thus maintaining the concentration gradient needed for osmotic movement of water. The mechanism recently proposed by Lundegardh (166) seems to be similar to that of Crafts and Broyer. A weakness of this theory is that it does not explain the presence of carbohydrates in the xylem sap. Hoagland (110) also emphasizes the relation between absorption of salts and occurrence of root pressure. Root pressure and guttation are exhibited only when root systems are in well aerated dilute salt solutions maintained at favorable temperatures. Guttation soon ceases from plants with roots immersed in distilled water or in unaerated solutions, conditions which also inhibit absorption of salt.

Some writers have emphasized the importance of the endo-

dermis in providing a sheath around the stele through which water can move only by passing through the protoplasm of the cells, but cannot pass through the suberized radial walls (55, 202). This is supposed to prevent leakage out of the stele under pressure and thus facilitate the development of hydrostatic pressure. Since passage cells with unsuberized walls usually occur opposite the xylem points, the writer considers the role of the endodermis to have been exaggerated.

The chief requisites for osmotic movement of water into the xylem are that the cortical cells be saturated and that the D.P.D. of the liquid in the xylem vessels be higher than that of the solution in contact with the roots. It has been demonstrated that water movement can occur across a multicellular living membrane even when the osmotic pressure of the cell contents of the membrane is much higher than the osmotic pressure of the solution inside the membrane (136). Various determinations of the osmotic pressure of the xylem sap previously cited indicate maximum values of one to two atmospheres which is materially higher than the osmotic pressure of most soil solutions. The highest osmotic pressures in the xylem sap of woody plants have usually been observed in the spring which is the season when root pressure also is usually greatest.

*c. Secretory versus osmotic theories.* Considerable discussion has occurred concerning the relative merits of the two types of explanations of root pressure and associated phenomena. It has been strongly argued that root pressure can be adequately explained as the result of osmosis, caused by a difference between the D.P.D. of the xylem solution and that of the medium surrounding the roots. Exudation is quickly stopped by immersion of roots in dilute solutions, and the rate of exudation of cotton is proportional to the difference between the osmotic pressures of the solution in the xylem and that surrounding the roots (77). Rapid reversal from exudation to absorption and back to exudation can be demonstrated by transfer of root systems from water to dilute sugar solution and back to water (145). Such reversal requires less than a minute, may be repeated numerous times, and is evidence that roots behave as very sensitive osmometers. It may be questioned that a complex secretory mechanism is capable of such rapid reversal.

The reviewer believes that osmotic movement of water occurs and that it is at least partly responsible for root pressure, but a simple osmotic theory is inadequate to explain periodicity in rate and pressure, or the reaction to auxin (238) and KCN (225, 250). Auxin applied to the stems increased the rate of exudation of garden pea and sunflower, and the effect of the auxin was exerted on the mechanism responsible for the diurnal periodicity of sunflower. It was suggested that auxin affects the utilization of food required for continued exudation, but no relationship could be established between exudation and respiration. It has also been suggested that auxin increases the absorption of water by plant tissue because it increases the intake of salts (47), but this view has not been supported by the most recent work (251). Electro-osmosis is not regarded as likely to prove a very important factor because conditions in roots are not regarded as favorable for adequate current flow (250).

On the basis of our present knowledge it seems reasonable to assume that the movement of water into the roots responsible for root pressure is largely dependent on the concentration of salts in the xylem. Accumulation of salts in turn is dependent on the metabolic activity of the living cells of the roots. Therefore factors affecting root metabolism might be expected indirectly to affect the intake of water and the resulting root pressure and exudation. This scheme accounts only for the salts present in the xylem sap and not for the carbohydrates which are often present.

It is likely that our views on this subject will be modified as our knowledge of secretory phenomena in plants and animals increases.

### *The Passive Absorption Mechanism*

It has been at least partly understood ever since the time of Hales that the forces bringing about absorption of water by transpiring plants are probably different from those causing root pressure. Sachs, Pfeffer and Strasburger agreed that transpiration sets in motion the forces which bring about water intake by transpiring plants. The picture was completed by the development of the cohesion theory of the ascent of sap which explained how the forces produced in the top by loss of water in transpiration could be transmitted through the water in the xylem to the

roots and there bring about the intake of water. Dixon (65) suggested that water may be regarded as moving through the transpiring plant along a gradient of decreasing vapor pressure from soil to roots, to leaves, and thence into the air. Renner (212) clearly differentiated between absorption brought about by forces originating in the roots and forces originating in the tops.

Evaporation of water from the mesophyll cells of the leaves produces a D.P.D. gradient which causes water to move into them from the xylem of the leaf veins. This reduces the pressure on the water in the xylem, and if transpiration is removing water more rapidly than it is being absorbed, as it often is, the water in the xylem is placed under tension. Subjecting water to tension lowers its vapor pressure and produces a D.P.D. numerically equal to the tension. Since there is a continuous liquid system extending through the xylem to the roots, this D.P.D. is transmitted to the roots and there produces a D.P.D. gradient along which water moves from the epidermis into the xylem. Some discussion has occurred concerning the relative importance of osmotic and imbibitional forces in absorption. Obviously water moves through both cell walls and vacuoles, and since they are in contact with each other the osmotic and imbibitional forces tend to come into equilibrium with each other (234). By discussing water movement in terms of D.P.D. gradients, argument on this subject can be avoided. If the tension in the xylem sap exceeds the osmotic pressure of the cortical cells of the root, the sap in these cells is also subjected to tension and the difference in D.P.D. exists directly between the soil and the epidermis, rather than between the soil and the xylem. Since the osmotic pressure of the root cells is usually rather low and since tensions of considerable magnitude are supposed to occur in xylem sap, it is probable that the root cells are frequently under tension.

Under these conditions roots act essentially as passive absorbing surfaces through which water is absorbed. That this is essentially true is indicated by the fact that shoots may remain alive for some days after their roots are killed (137) and that water intake by a root system can be greatly increased by attaching a vacuum pump to the stump (128, 136, 213). Various aspects of this problem are discussed in the following papers (141, 157, 235).



*Relative Importance of Active and Passive Absorption*

Considerable evidence is available concerning the relative importance of active and passive absorption in the water economy of plants. In the first place there are many species, including the gymnosperms, which are not known to exhibit root pressure or other evidences of active absorption. Furthermore, among those species in which root pressure is of regular occurrence it is seldom observed in transpiring plants. Water and dye are commonly absorbed through incisions made into the xylem of transpiring plants, but water rarely exudes until after an appreciable interval, if at all. When the tops are removed from freely transpiring plants, usually no immediate exudation occurs from the stumps, but water is absorbed for a period varying from a few minutes to a few hours (141). Exudation apparently begins only after the root cells have become fully turgid by absorption of water through the stump and from the soil.

Perhaps the most important evidence concerning the relative importance of active and passive absorption is a comparison of the volume of water exuding from a detopped root system with the volume lost in transpiration by the same plant prior to removal of the top. In one series of experiments the volume of exudation from stumps of potted coleus, hibiscus, balsam, sunflower and tomato plants was only 1% to 5% of the volume of water lost by the intact plants in transpiration (141). Even when a vacuum pump was attached to the stumps the volume of exudation rarely equalled the volume lost in transpiration by intact plants (141, 213, 254). It has been suggested (132, 218) that the tension produced by transpiration stimulates the root cells and increases active absorption, but no evidence of root pressure has been found in the roots of transpiring plants (19). In fact removal of the root system is often followed by a considerable temporary increase in the rate of absorption by transpiring shoots (140).

Renner (211) long ago presented evidence that the forces developed by transpiring shoots are much more important in water intake than the forces developed in the roots. Considerable evidence is available indicating that root systems are unable to absorb water from as concentrated solutions as are intact plants. The absorbing power of a detopped root system is relatively low.

Maximov (179, 53-55) cites Russian work (227) in which it was found that exudation from the stumps of various species of plants was generally stopped by solutions with an osmotic pressure of 0.5 to 1.5 atmospheres. Exudation from the stumps of sunflower, castor bean and bean was stopped by sucrose solutions with osmotic pressures of 1.6 to 4.2 atmospheres (213). While intact bean plants could absorb from solutions with osmotic pressures up to 14.6 atmospheres, their root systems could absorb from solutions with osmotic pressures no higher than 1.9 atmospheres (245). The effects of dilute solutions in hindering or even reversing the movement of water through root systems has been observed by several other investigators (77, 136, 141, 213, 221). Detopped root systems do not exhibit exudation in soil drier than about half way between the moisture equivalent and the permanent wilting percentage, but exhibit exudation as soon as the soil is wetted (145). Evidently about half the soil moisture available to an intact plant is unavailable to the root system alone. There is also both direct and indirect evidence that the active absorption mechanism often fails to function in saturated soil.

Renner (213) estimated that the roots of transpiring sunflowers develop absorbing forces of 4 to 11 atmospheres, and another worker (132) estimated that a force of 20 to 73 atmospheres must be developed to bring about intake of the volume of water required by a transpiring sunflower. These estimates are probably too high because it has since been learned that as the tension on the water in the xylem increases the area of root surface through which water intake occurs also increases (28). Increasing the area through which absorption occurs materially decreases the force required to absorb a given volume in a unit of time. Warne (254) estimated the tension in the xylem elements to vary from 1.2 atmospheres in *Pelargonium* to 13.1 atmospheres in *Erica*. In general, when transpiration was high the greatest tensions were found in xerophytes and the lowest in mesophytes and succulents. As would be expected, the tensions were reduced or disappeared when the plants were well supplied with water and transpiration was stopped. Since the D.P.D. of soil at the permanent wilting percentage is in the neighborhood of 15 atmospheres (214), it is clear that all transpiring plants must be capable of absorbing water against a deficit at least this great. The root system alone,

however, can absorb only against a D.P.D. of one or two atmospheres.

One reason often given for emphasizing the importance of the metabolic activity of root cells in water intake is that absorption is materially reduced by low temperature and by poor aeration, both of which are known to reduce the rate of respiration. It appears possible, however, that the physical effects of low temperature and poor aeration are sufficient by themselves to explain decreased absorption by transpiring plants (142, 144). This phase of the problem will be discussed with factors affecting absorption.

It is concluded that active absorption, as evidenced by exudation and root pressure, is wholly inadequate to supply the water requirements of transpiring plants. It is probable that active absorption does not even supplement passive absorption in rapidly transpiring plants because none of the suggested mechanisms for active absorption would operate unless the cells of the roots were turgid. Water absorption by transpiring plants apparently is caused by forces set in motion by the loss of water in transpiration. Removal of water by transpiration decreases the pressure or causes tension on the xylem sap, producing a gradient of decreasing pressure and increasing D.P.D. along which water moves from the epidermis to the xylem of the roots. The roots act as passive absorbing surfaces in connection with this mechanism, and it may be said that water is absorbed through the roots of transpiring plants rather than pumped into the plant by the roots.

#### FACTORS AFFECTING ABSORPTION

The factors affecting the rate and amount of absorption may be grouped as plant factors, such as rate of transpiration and extent of the root system, and environmental factors, such as soil moisture, temperature, aeration and concentration of the soil solution.

##### *Plant Factors*

*Rate of transpiration.* If transpiration produces the forces chiefly responsible for the intake of water we would expect the rate of absorption to be closely related to the rate of water loss. A number of studies made at various times and under a variety

of conditions have in general shown a close correlation between the rates of these two processes (150, 159, 190, 252). The writer (139) made simultaneous measurements of absorption and transpiration of loblolly pine, green ash, yellow poplar, black willow, sunflower and opuntia. Sunflower was grown in both soil and water culture, willow in water culture and the other species in soil. In all instances changes in rate of water loss were soon followed by similar changes in rate of water intake. The fact that changes in transpiration precede changes in rate of absorption indicates the close dependence of absorption on transpiration.

*Root system. a. Absorbing zone.* The region of maximum water intake by a root is determined by its anatomical structure. This changes with age in such a manner that the principal absorbing zone is generally supposed to be restricted to the youngest region, near the root tip. Since the anatomy of roots is adequately described in various texts (74, 99, 184), it will not be discussed in this paper.

Several studies have been made of the relative volumes of water absorbed by various regions of the root. Coupin (51, 52) believed that absorption occurs chiefly through the root tips, but it is generally agreed that little water is absorbed through the root cap and meristematic region (29, 113, 203, 237). The exact location of the zone of most rapid absorption varies with the length and age of the root (220), with time (222) and with the tension developed by the transpiring shoot (28). Rosene (220), working with onion roots, found that maximum absorption occurred at the base of roots less than 50 mm. long, but in roots over 70 mm. long maximum absorption occurred 40 to 60 mm. from the apex and decreased toward tip and base. Removal of part of the roots increased the rate of absorption by the remaining roots. Considerable fluctuations in rate of absorption in adjacent areas of onion roots were also observed (222). Absorption by corn roots is said to increase to a maximum about 10 cm. back of the root tip and then usually to decrease proximally in roots more than 10 cm. long (101). It has been observed that the absorbing zone of broad bean is a few centimeters back of the tip with absorption decreasing in each direction from this zone. When the shoot is transpiring rapidly the absorbing zone is extended toward the shoot, including the entire unbranched region (28, 29). It was



suggested that this results from changes in permeability produced by increased tension in the xylem, but it seems more probable that the high tension in the xylem during periods of rapid transpiration causes water intake through tissue which has too high a resistance to water movement to permit entrance at lower tensions.

It has long been assumed that root hairs materially increase the absorption of water by increasing the absorbing surface, but their importance has been questioned by a few workers (51, 52, 113). The zone of maximum absorption as reported by most workers corresponds with the root hair zone, or at least the zone where root hairs would be present if they had developed. Rosene (224) made direct measurements showing that water intake occurs through root hairs of radish with about the same velocity as through the hairless epidermal cells of onion roots. Root hairs have been estimated to increase the absorbing surface of the roots bearing them from five to 20 times (184). The total surface of the root hairs on a four-month-old winter rye plant was 1.6 times the total root surface exclusive of root hairs (64). Root hairs ordinarily live only a few days, but persistent root hairs have been observed on Valencia orange seedlings (103), *Cercis*, *Gleditsia Gymnocladus* (173) and Venus fly trap (236), and root hairs three years old were reported on certain composites (264). It may be questioned that these persistent root hairs function in absorption, as their walls often become thickened and even suberized and lignified. The absorbing surface of some root systems, especially those of trees, is frequently modified by development of mycorrhizal structures through which much absorption of water and minerals is believed to occur (97, 98).

The epidermis and its root hairs are usually soon destroyed. Sometimes the hypodermis develops a suberized layer which is later followed by another such layer produced from a phellogen originating in the pericycle. In the Valencia orange the hypodermal cells sometimes produce secondary root hairs, lenticels and absorbing areas consisting of groups of thin-walled radially elongated cells (103). Water is presumably absorbed through all of these structures. Usually during secondary growth activity of a phellogen developed from the pericycle encloses the root in a layer of cork and thereby destroys the cortex. The presence of

such a sheath of suberized tissue would be expected to prevent the entrance of water and solutes, but this does not seem to be true. Since at certain seasons, as when the soil is cold or dry, few or no growing root tips can be found on woody species it has been inferred that absorption must occur through the older suberized portions of such roots (39, 56, 194). No direct experimental evidence was presented until recently when it was demonstrated by a potometer study that water can be absorbed through the suberized portions of roots of sour orange (101). The writer (147) recently made a number of measurements of water absorption through attached suberized roots of pine and hardwoods varying from three to 20 mm. in diameter and found measureable absorption to occur through all sizes of roots. It has also been demonstrated that water can be absorbed through dead root systems so long as their conducting tissues remain unplugged (137).

*b. Extent of root systems.* Since the principal zone of absorption is often near the root tip the number of tips is an important factor in absorption. Furthermore, the continual extension of these root tips through the soil is frequently essential to absorption of adequate quantities of water. This is because in soils with a moisture content below field capacity capillary movement of water toward roots is very slow. The moisture content of the soil in contact with an absorbing root therefore tends to be reduced to the permanent wilting percentage, and unless it is rewetted new supplies of moisture become available only as the roots penetrate into new areas of soil. Contact between roots and soil particles is also believed to facilitate the absorption of minerals (124). Roots elongate fairly rapidly, a rate of 0.5 in. per day being common in grasses, and corn roots are reported to grow downward at the rate of 2 to 2.5 in. per day for three or four weeks (255). Roots of loblolly and shortleaf pine were observed to grow an average of about 0.1 in. per day under favorable conditions (210).

The literature dealing with the extent and development of root systems is too extensive to be reviewed or even cited adequately in this review. The outstanding investigations are by Weaver and his co-workers, and the reader is referred to their publications for extensive bibliographies on roots and root systems (255, 256, 257, 260). Miller (186) has also summarized much information

concerning factors affecting the development of root systems. A few papers will be discussed. One of the earlier measurements of the extent of root systems was by Clark (42). He found a squash grown in a greenhouse bench to have 84,000 feet (15.9 miles) of roots of which he estimated that 50,000 feet had been added at the rate of 1,000 feet per day. The number and extent of roots is especially great on grasses. A wheat plant grown without competition was found to have 44 miles of roots, a rye plant 49 miles, and a wild oats plant 54 miles (196). Winter rye plants grown four months in boxes of soil in the greenhouse were estimated to have over 13 million roots with a total length of over 387 miles and a surface of 2,554 square feet. These roots bore over 14 billion root hairs with a total length of 6,603 miles and a surface of 4,321 square feet (64). There was an average daily addition of 3.1 miles of roots to each plant. It has been estimated that this rate of root extension would make available 1.6 liters of water daily in a sandy loam at field capacity and 2.9 liters in a heavy clay (149). The root surface of these plants was about 130 times the shoot surface.

*c. Factors affecting development of root systems.* The general physical and physiological characteristics of root systems, like those of other plant organs, depend primarily on their heredity. Nevertheless, wide variations in development of root systems within the limits of their hereditary potentialities are brought about by variations in certain environmental factors. Among these are soil moisture and aeration which are interrelated and in turn are affected by soil texture and structure, soil fertility, soil temperature and competition with other root systems.

Root competition between plants of the same or of different species usually reduces the extent of the competing root systems. Wheat and barley develop root systems nearly 100 times larger when grown without competition than when grown in drill rows six inches apart (196). Planting corn between rows of young apple trees greatly reduced the extent of the root system of the apples, both laterally and vertically (273). Competition with grass reduces the amount and extent of root systems of forest tree seedlings (261), and the vigor and size of root systems of loblolly pine seedlings are reduced by competition with forest vegetation (45). Such competition is quite complex, including

the effect of shading on the processes occurring in the shoots and competition for water and minerals by the roots.

Moisture content of the soil is perhaps the most important environmental factor affecting root development because either too much or too little soil moisture hinders development of roots. It has been claimed that roots are able to grow into dry soil, possibly by transferring water from roots growing in moist areas (26, 27, 231). Other investigators, however, have found roots unable to penetrate more than a few millimeters into dry soil from adjacent moist soil (62, 106, 162), and it seems unlikely that they make appreciable growth into soil at or below the permanent wilting percentage. In the Great Plains region, for example, root penetration is definitely limited by the depth to which water penetrates (258). Hydrotropism is apparently less important in roots than once supposed, being completely absent from some species and weak in others (162).

Everyone is familiar with the yellowing of leaves, reduction in growth and eventual death of crop plants resulting from prolonged saturation of the soil with water. That this damage is caused by injury to the roots from lack of oxygen and possibly by accumulation of carbon dioxide rather than by the direct effects of water is indicated by the satisfactory growth of such species in well aerated water cultures. It is said that saturated soils containing organic matter also usually develop toxic concentrations of ferrous iron, sulfides and manganese (216). In general, the best developed root systems occur in soils with a moisture content which is usually below field capacity but not as low as the permanent wilting percentage. Within certain limits, therefore, root growth is inversely proportional to the moisture content of the soil (71, 114).

Respiration of roots and soil organisms tends to decrease the oxygen content and to increase the carbon dioxide content of the soil atmosphere and of the water films in equilibrium with it. The activity of soil organisms in this respect is affected by temperature, moisture and the supply of nitrogen and carbohydrates. By adding starch and ammonium sulfate to soil such an increase in soil fungi was caused that all free oxygen disappeared and wheat plants growing in it were killed (129). The concentration of gases in the soil atmosphere tends to become equalized



with that of the above-ground air chiefly by diffusion. Aeration is related to soil texture and structure because gas exchange ordinarily occurs through the larger or non-capillary pores which are free of water at moisture contents lower than the field capacity. Aeration is better in coarse-textured sandy soils than in fine-textured clays. This explains the fact that while root systems penetrate five to 35 feet into the light well drained soils of Nebraska and surrounding States, most roots are restricted to the top two or three feet in the East where heavy clay subsoils hinder drainage and aeration. Roots developed during periods of low soil moisture sometimes die after rains or irrigation raise the moisture content too high for good aeration (24, 118).

The earlier work on aeration and root growth has been summarized by Clements (43), and various aspects of the problem are discussed in the following papers which also give numerous references (22, 36, 160, 186, 257, 259). According to Cannon (36), many roots will make slight growth at 0.5% to 2.0% of oxygen, but 8% to 10% is usually necessary for good growth. He found that a higher oxygen concentration is necessary for optimum growth at high soil temperatures than at low temperatures. Apple tree roots can survive for some time at 55° F. to 70° F. in soils containing 0.1% to 3% oxygen (23), but growth was so seriously checked below 10% of oxygen that top growth was noticeably reduced (21). In New York there is said to be a relatively short period of time when enough oxygen for good root growth occurs in clay soils below three feet (24). Flooding the soil around the roots of young apple trees greatly reduced transpiration and photosynthesis, but increased respiration of the tops (40, 229).

Most species require good aeration for proper development and functioning of their root systems, but certain species characteristic of bogs and swamps can survive for long periods in saturated soil. Apparently the root systems of such species can survive with little or no oxygen and probably are able to carry on anaerobic respiration without suffering injury (151, 158). It also seems probable that considerable oxygen diffuses down from the aerial parts to the submerged roots and rhizomes of some species (50, 86, 152). Part of this oxygen probably is released by photosynthesis in the shoot (37, 152). It is well known that most bog

plants have shallow root systems, and some are so rooted on hummocks of sphagnum that their roots are fairly well aerated (53). Trees on poorly drained uplands also sometimes have very shallow root systems (25).

While the roots of many plants will grow during the entire year, growth is usually much slower during winter. Apple roots have been observed to make some growth at depths of 3.5 to 4.5 feet in soil near freezing while the upper two feet were frozen and subzero air temperatures occurred (46). More roots and a higher root-shoot ratio were obtained in white pine seedlings in soil at 88° F. than at any lower temperature (1). Several investigators have observed that while the root growth of trees and other perennials is reduced in winter it does not completely cease unless the soil is frozen (35, 93, 172, 210, 217, 248). Under some conditions temperatures near the surface of the soil may be high enough to injure roots or the lower part of the stems of tree seedlings (11, 134, 197, 233). Very few roots occur in the upper foot of soil in certain California orchards because of the high soil temperatures during summer (205). Some species of grasses show a definite periodicity in root growth which may be in part related to soil temperature and flowering (244).

Roots tend to branch more profusely in very fertile soil than in soil low in available minerals (257). Their development is also generally believed to be affected by soil acidity, though recent work indicates that good plant growth is possible in nutrient solutions over a wide pH range if care is taken to insure the availability of all necessary minerals (6). In arid regions accumulation of salts in toxic concentrations often injures roots and prevents establishment of plants (76, 100, 175, 176).

Since roots are dependent on their shoots for a supply of carbohydrates those factors which affect the amount of photosynthesis also affect root growth. Thus heavy grazing or frequent clipping is well known to reduce the size of the root systems (16, 95, 195, 215). It has also been demonstrated that shading reduces growth and the ratio of roots to shoots in tree seedlings (15, 34, 83, 184, 198).

#### *Environmental Factors*

*Readily available moisture content of the soil.* Since the terminology and the relation of soil moisture to plant growth has

been considered at length in an earlier review (148), it will be discussed but briefly in this paper. Only that portion of the soil moisture which lies above the permanent wilting percentage is available for plant growth. Permanent wilting of plants may occur at less than 1% of water on a dry weight basis in coarse sand, and at 25% or higher in clay. The moisture content of a soil, therefore, can be intelligently interpreted in respect to plant growth only by considering its relation to the permanent wilting percentage and the field capacity of that soil. Some investigators claim that soil moisture is equally available to plants over the range from field capacity to permanent wilting percentage, but there is considerable evidence that the availability of water decreases with decreasing soil moisture from at least half way down the range from field capacity to permanent wilting percentage (145, 148). Some data are available indicating that transpiration decreases with soil moisture contents both above and below the field capacity (184, 266), and this is also true of exudation from detopped root systems. A soil moisture content above the field capacity doubtless depresses absorption by hindering proper aeration of the roots. Decreasing soil moisture content decreases absorption because as the moisture content decreases and the films of water surrounding the soil particles become thinner they are held more firmly. The diffusion pressure deficit of the soil moisture is only about one-half to one-third of an atmosphere at the field capacity, but it is about 15 atmospheres at the permanent wilting percentage.

As the steepness of the diffusion pressure deficit gradient from soil to roots decreases, water movement slows down until finally absorption lags so far behind water loss that wilting occurs. Absorption does not completely cease, however, until the plant dies of desiccation. Movement of water in soils below their field capacity is so slow that it becomes available to plants only if the roots actually come into contact with it. Puri (207) suggested that it is doubtful that the permanent wilting percentage is determined by the decreased D.P.D. gradient from soil to roots. Rather, he believes, it is determined by the amount of moisture held in capillaries too small to be penetrated by root hairs. Thus in fine-textured clay soils with numerous small capillaries more water is unavailable than in sandy soils with few very small

pores. As the soil moisture content decreases and absorption becomes slower, growth is checked, and decreased elongation of root tips probably further decreases absorption.

There is some evidence that soil moisture near a plant is more available than that at a distance, even though the latter is in soil occupied by the root system. For example, the moisture in soil four feet from corn plants was not absorbed until the moisture content of the soil near the plant was reduced below the permanent wilting percentage (62). Results obtained with sorghum under field conditions are indicative of somewhat similar behavior (49). Interpretation of the results of such experiments is complicated by the tendency toward a higher concentration of roots in soil near the plant than at a distance.

*Soil aeration.* Inadequate soil aeration with resultant oxygen deficiency and carbon dioxide accumulation decreases absorption directly, and also indirectly by reducing root growth. The earlier work on aeration in relation to absorption has been discussed by Clements (43). The importance of proper aeration of soil and water cultures as essential to maximum absorption of both minerals and water has been emphasized in recent papers (5, 110). It is suggested that, generally, even in the best aerated soils, growth of species with a high oxygen requirement is probably limited by lack of oxygen and possibly by accumulation of carbon dioxide. Gilbert and Shive (85) concluded that the oxygen content of water in equilibrium with the air is not high enough for maximum growth of some crops. There are considerable differences in oxygen requirements of roots of various plants, the optimum concentration for tomato being so high that it was toxic to soybeans (85). Injury to tomato roots from excessive aeration at high temperatures has been observed (5), and other workers have reported injury from excessive aeration (160).

Tomato plants growing in unaerated tanks were observed to wilt on warm days, but recovered when air was bubbled through the tank (5), and several other examples of reduction in water intake by plants with roots in poorly aerated media have been published (145). Little information is available, however, concerning the relative importance of oxygen deficiency and accumulation of an excess of carbon dioxide. In India several species of trees were quickly injured or killed by development of a heavy



sod over their root systems, and it was concluded that at least part of this injury resulted from an excess of carbon dioxide produced by the grass roots (115). The writer (142) found that saturating the soil or water surrounding the roots of tomatoes and sunflowers with carbon dioxide reduced transpiration one-third to one-half within an hour. Saturating the water around the roots with nitrogen reduced transpiration less than 10%. Exudation from detopped root systems was reduced about two-thirds by carbon dioxide, but only about 10% by nitrogen. Exudation from root systems attached to a vacuum pump was reduced one-third to one-half by carbon dioxide, but only 10% by nitrogen. These results seem to indicate that absorption was reduced more in the first two hours by an excess of carbon dioxide than by a deficiency of oxygen. The large reduction in water intake by roots of transpiring plants and root systems attached to a vacuum line indicated that carbon dioxide decreases the permeability of the protoplasmic membranes of the roots of these species to water. Hoagland and Broyer (111) reported that a high concentration of carbon dioxide in the solution surrounding the roots abruptly decreased absorption of both bromide and water by roots attached to a vacuum pump. Later absorption of bromide and water increased. Apparently carbon dioxide first decreased permeability but later so injured the protoplasm that permeability to water and salts was increased. Bubbling nitrogen through the solution around the roots decreased permeability, but there was no subsequent increase. This presumably is a reaction to oxygen deficiency. Chang and Loomis (38) reported that bubbling  $\text{CO}_2$  through the solution surrounding the roots of maize, rice and wheat decreased absorption of water and minerals, but  $\text{N}_2$  did not affect absorption. They concluded that  $\text{CO}_2$  has specific effects on absorption of water and solutes.

There is some evidence, however, that over periods of more than a few hours, oxygen deficiency may be more important in reducing absorption than is accumulation of carbon dioxide. Plants of coleus, corn, cotton, sunflower, tobacco and tomato were grown (267) in sand-filled containers arranged for aeration with various gas mixtures. The mixtures used were compressed air, 20%  $\text{CO}_2$  plus 20%  $\text{O}_2$  plus 60%  $\text{N}_2$ , pure  $\text{N}_2$ , and 20%  $\text{CO}_2$  plus 80%  $\text{N}_2$ , and the roots were aerated at a rate of two liters

per plant per hour for seven to 14 days. Lack of oxygen decreased transpiration of all species and caused death of many roots of coleus, tobacco and tomato. Aeration with 20%  $\text{CO}_2$  in the presence of  $\text{O}_2$  did not reduce transpiration of corn, cotton or sunflower, and only slightly reduced that of coleus, tomato and sunflower. An excess of  $\text{CO}_2$  in the absence of  $\text{O}_2$  reduced transpiration of most species little more than  $\text{O}_2$  deficiency alone, but coleus was killed in five days, and transpiration of tomato was decreased more by  $\text{CO}_2$  alone than by  $\text{O}_2$  deficiency alone or by  $\text{CO}_2$  plus  $\text{O}_2$ . Growth was also reduced more by  $\text{O}_2$  deficiency than by an excess of  $\text{CO}_2$ .

Injury to root systems when poorly aerated presumably largely results from accumulation of toxic products of anaerobic respiration. The lower energy output of anaerobic respiration may also be responsible for decrease in active absorption of water and decreased intake of minerals. Possibly this decrease is partly the result of decreased permeability. It has been suggested that permeability is related to metabolism because maintenance of protoplasmic membranes is dependent on metabolic activity. Apparently permeability, metabolism, salt accumulation, and possibly active absorption of water are closely related (111). Reduction in or cessation of active absorption cannot explain the large reduction in absorption of transpiring plants, however, because active absorption can supply only a small percentage of the water needed by rapidly transpiring plants. The reduced absorption by inadequately aerated roots of transpiring plants must result from decreased permeability of the roots and from decrease in absorbing surface caused by death of rootlets and cessation of root growth.

*Soil temperature.* It has been known at least since the time of Sachs that low soil temperature reduces the absorption of water by plants and that not all species are affected to the same extent. In general, as might be expected, plants which are native to warm climates and normally grow in warm soil exhibit a greater reduction of water intake when the soil is cooled than do plants which normally grow in cool soils. An extensive comparison of various species was made by Döring (70) whose data indicate that water intake of plants from northern flat moors and high moors was reduced less at low temperatures than was water intake

of plants from warmer and drier soils. Firbas (79) also found that high moor species absorb water freely at low temperatures. Water absorption by Bermuda grass, a native of warm regions, was sufficiently retarded at 10° C. to cause wilting, while bluegrass was unaffected at this temperature (30). The writer (146) found that watermelons and cotton, which are warm season crops, absorbed only 20% as much water at 10° as at 25° C., while Georgia collards, a cool season crop, absorbed 75% as much water at 10° as at 25° C. Loblolly and slash pine, which are southern species, absorbed only 40% as much water at 10° as at 25° C., while the northern species, red and white pine, absorbed 60% as much. Kozłowski (135) found that low soil temperatures reduced transpiration of loblolly pine more than that of white pine. Reduction in water intake at temperatures well above freezing has been reported for a number of species, including citrus fruits (14, 90), cotton (4), cucumbers (230), muskmelons (209), sugar cane (72), sunflowers (44) and willow (206). Serious injury to cucumbers has been reported as a result of watering greenhouse beds with cold water in winter (230), and a chlorosis of greenhouse-grown gardenias was found to occur only in soil cooler than 18° C. (127). Cold soil may be of some ecological significance with respect to plant distribution, and winter injury may sometimes result from desiccation caused by inadequate water absorption from cold soil in sunny weather (185, 226).

It is not surprising that soil temperature often exerts such a marked influence on water intake, since it can be affected in a number of ways by low temperature. Cold soil retards root elongation and thereby reduces root penetration into new soil masses, a matter of importance in soils below their field capacity. The water-supplying power of the soil, as measured by soil point cones, is only one-third to one-half as great at freezing as at 25° C. (138). The viscosity of water is twice as great at 0° as at 25° C., and the vapor pressure is only one-fifth as great. The viscosity of protoplasm is three or four times greater near freezing than at room temperature (262), resulting in greatly increased resistance to water movement through the cell membranes. The writer found active absorption as measured by exudation from detopped sunflower and tomato root systems to be most

rapid at 25° C. It decreased at higher and at lower temperatures, ceasing at about 12° in tomatoes and about 2.5° C. in sunflowers. Wilting of transpiring plants in cold soil cannot be attributed to decrease in active absorption because it normally supplies so little water to the top. It was found, however, that water movement through root systems in soil and in water attached to a vacuum pump was less than one-fifth as great at freezing as at 25° C., indicating that there is a high resistance to water movement through the roots at low temperatures. Water movement through dead roots was about half as great at freezing as at 25° C., indicating that the resistance was decreased but not eliminated by destruction of the protoplasmic membranes. In view of these results it is concluded that the principal cause of decreased water absorption by transpiring plants at low soil temperatures is increased resistance to water movement across the living cells, resulting from the combined effects of decreased permeability of the root membranes and the increased viscosity of the water itself (144).

*Concentration and composition of the soil solution.* Absorption of water depends primarily on the existence of a diffusion pressure deficit gradient from soil to roots. The plant is potentially capable of developing a D.P.D. at least equal to the osmotic pressure of its cells. This averaged 14.4 atm. for plants from the vicinity of Cold Spring Harbor, N. Y., and much higher for plants of dry habitats (94). Furthermore, as the soil moisture content decreases, the osmotic pressure of the plant tissues increases, thus tending to maintain a gradient from soil to roots (109, 133, 171, 177, 186, 242). The D.P.D. of the soil moisture is the sum of the pressure potential (capillary potential) of the soil moisture and the osmotic pressure of the soil solution.

In most cultivated soils the osmotic pressure of the soil solution is negligible, but sometimes it is so high as to inhibit plant growth. This occasionally occurs in greenhouse soil as a result of excessive applications of fertilizer (48). It is highest in arid regions where rainfall is insufficient to leach away the salts accumulated near the surface by evaporation of water. In the western states best yields are obtained on soils with an osmotic pressure of less than two atmospheres. Good yields of some species are obtained up to an osmotic pressure of four atmos-



pheres, but growth and yield decrease rapidly with increasing concentration. At concentrations higher than 40 atmospheres all species fail to grow (176). Because of the agricultural importance of this problem much work has been done on the effects of salt concentration on the growth of crop plants. Increased salt concentration has been shown to decrease transpiration and water requirement (75, 182), absorption of water (76, 104, 161, 221) and growth of various species (8, 102, 176). Although plants grown in media high in salt are reduced in size and yield, they often have a higher water content than plants grown in media low in salt (102, 182, 253). There are several causes for the decreased absorption of water in the presence of salts besides the increased D.P.D. of the soil solution. Perhaps the direct osmotic effects on absorption are less important than the effects on the extent and efficiency of the root systems. Root growth is inhibited at high salt concentrations (76), and roots are unable to extend into new soil masses. Furthermore, these slow growing roots tend to become suberized to their tips (104) and thus possess less efficient absorbing surfaces than rapidly growing roots.

The osmotic pressure of the soil solution is apparently more important than the type of ions present. Root growth and water uptake of corn and tomato were affected to the same extent in a complete nutrient solution and a chloride solution of the same osmotic pressure (76). Peach trees were found to tolerate slightly more sulfate than chloride, but the difference was small (103a). It was suggested by Meyer (182) that the differences which he observed in retarding effects of various salts on transpiration might largely be caused by differences in osmotic pressure of equimolar solutions rather than by specific ionic effects. Possible differences in effect on permeability of cell membranes cannot entirely be overlooked, however. Solutions of 0.01 M HCl and NaOH were found to retard water absorption by willow (269).

#### WATER ABSORPTION IN RELATION TO OTHER PROCESSES

##### *Relation of Intake of Solutes to Intake of Water*

Most of the early physiologists supposed that absorption of minerals was proportional to the absorption of water, although

very little experimental evidence was presented. Later, various species of plants were grown under conditions favoring high and low rates of transpiration and their salt contents compared (33, 89, 96, 131, 174, 180, 192). The results of these experiments indicate that the volume of salts absorbed is not proportional to the volume of water. Such experiments are not conclusive because plants grown in sun and shade or with high and low humidity are anatomically and physiologically different and cannot properly be compared. In certain recent experiments this objection was eliminated by exposing plants to high and low humidity for only three or four days and comparing salt and water intake (81, 272). In these experiments there was some increase in salt absorption with increased absorption of water, but different ions were not absorbed at the same rate, and the rate of absorption of various ions differed in different species. Hoagland and his colleagues have emphasized the dependence of salt absorption and accumulation by roots on the metabolic activity of the root cells (110, 111). They have shown that excised barley roots can absorb as much salt in a short period of time as similar intact transpiring plants. In other experiments plants supplied with minerals only at night when transpiration was low absorbed as much salt as plants with their roots in nutrient solution only during the day or during the entire 24 hours. These and other experiments indicate that while transpiration may not be without effect (31), the quantity and kind of ions absorbed is usually determined by the metabolic activity of the roots rather than by the volume of water absorbed (110).

#### *Absorption in Relation to Other Processes*

The relation between rate of absorption and rate of transpiration is more important than the absolute rate of either process because it determines the internal moisture content of plants and thereby profoundly affects many physiological processes. Although there is relatively little resistance to water movement through the xylem itself (254, 269), there is considerable resistance to movement through the mass of living cells lying between the epidermis and xylem of the roots (140). As a result, on days when transpiration is rapid, absorption lags so far behind transpiration that the moisture content of the plant is ma-

terially reduced and wilting often occurs, even of plants in moist soil or in well aerated liquid cultures. Well defined diurnal variations in moisture content result, especially in the leaves. On a typical day, moisture content decreases during the morning and early afternoon and reaches a minimum in the late afternoon. It then increases during the night, reaching a maximum about midnight or later (139, 240). Accompanying this diurnal variation in water content is a similar variation in the osmotic pressure and D.P.D. of the leaves (107, 242). Considerable redistribution of water may occur between various tissues of a plant as a result of local water deficits. Best known is the removal of water from fruits by transpiring leaves (10, 168). Water is also removed from mature cotton bolls during periods of rapid transpiration, but not from immature bolls (2).

Water deficit affects other internal processes and conditions which profoundly influence the growth, development and even the survival of the plant. Among them are stomatal opening, rates of transpiration, photosynthesis and respiration, the starch-sugar equilibrium, and cell division and enlargement (117, 184, 179).

#### SUMMARY

Intake of water apparently is brought about by two independent processes differentiated by Renner as the active and passive absorption processes. When soil moisture is abundant and transpiration slow, absorption often exceeds water loss, resulting in the development of positive pressure or "root pressure" in the xylem. This pressure causes guttation and exudation phenomena. Since the absorption mechanism responsible for root pressure is dependent on the presence of active living cells in the roots, it is termed "active absorption". Some workers believe root pressure is caused by secretion of water into the xylem by the surrounding living cells. Others believe it is a relatively simple osmotic phenomenon caused by a difference in concentration of solutes in the xylem elements and in the solution surrounding the roots. Certain similarities between the conditions necessary for salt accumulation and for development of root pressure suggest that they are interrelated to the extent that the occurrence of active absorption and root pressure are at least partly dependent on the accumulation of salt in the xylem and so

indirectly related to metabolic activity and the permeability of the root cells.

During periods of rapid transpiration or when soil moisture is deficient no root pressure occurs. Instead, the water in the xylem is under reduced pressure or even tension. This increases its diffusion pressure deficit and produces a gradient of increasing diffusion pressure deficit and decreasing pressure along which water moves from the external solution into the xylem. Since under these conditions the roots act simply as absorbing organs and water intake appears to be independent of any secretory or osmotic activity of the root cells, this type of water absorption is termed "passive absorption".

Active absorption ordinarily can supply less than 5% of the water required by a rapidly transpiring plant. It does not occur from as dry soil nor from as concentrated solutions as does passive absorption of transpiring plants. Some species never exhibit any root pressure or other evidence of active absorption. It is therefore concluded that the root pressure or active absorption process is of negligible importance in supplying water to plants.

The rate of absorption of water by plants in moist soil is determined primarily by the rate of transpiration. It is affected to a lesser degree by the extent and efficiency of the root system. Important environmental factors affecting absorption of water are the available moisture content of the soil, concentration of the soil solution, soil aeration and soil temperature.

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